PAN-PACIFIC ENTOMOLOGIST
63(3), 1987, pp. 237–241

Ecology of *Rhopalomyia californica* Felt at Jasper Ridge (Diptera: Cecidomyiidae)

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Abstract.—An ecological study of *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae) was conducted at the Jasper Ridge Biological Preserve (Stanford University) during 1982–83. The midge, which develops in terminal galls on *Baccharis pilularis* DC, was relatively rare throughout the course of the study. Analysis of life-table data suggested that its predators and parasites played a major role in maintaining population density at comparatively low levels. The parasite guild consisted of seven hymenopteran species: *Torymus koebelei* (Huber) & *T. baccharidis* (Huber) (Torymidae), *Zatropis capitis* Burks & *Mesopolobus* sp. (Pteromalidae), *Tetrastichus* sp. (Eulophidae), *Eupelmus inyoensis* Girault (Eupelmidae), and *Platygaster californica* (Ashmead) (Platygastridae). Malathion-bait sprays applied to an adjacent area (Woodside) not only resulted in a massive midge outbreak, but also indirectly altered the spatial structure of the midge population. It is suggested that *R. californica,* when introduced without its natural enemies, may be an important biological-control agent against weedy *Baccharis* spp. in Texas and Australia.

Rhopalomyia californica Felt is a native cecidomyiid midge which develops in multi-chambered, terminal galls on *Baccharis pilularis* DC in California. Tilden (1951b) described the natural history of the midge and most subsequent investigations have dealt largely with the midge and its parasites as a model system for addressing basic issues in community ecology and applied biological control (Doutt, 1961; Force, 1974; Ehler 1982, 1985; and Hopper, 1984). The latest development concerns the use of *R. californica* as a biological-control agent for related *Baccharis* spp. which are rangeland weeds. In this regard, the midge is now well established in Queensland, Australia, where it shows considerable promise for eventually controlling *Baccharis halimifolia* L. in many parts of its range (McFadyen, 1985; W. A. Palmer, pers. comm.). It was also introduced into Texas during 1985 and 1986 (for control of several *Baccharis* spp.) and is now established at certain release sites (P. Boldt, pers. comm.).

The purpose of the present paper is to summarize available data on the ecology of *R. californica* at one site in its native range (Jasper Ridge Biological Preserve) in order to facilitate eventual comparative studies in Texas and Queensland. Details of the study sites, materials, and methods were given by Ehler et al. (1984).

Analysis of Life-Table Data

From 30 March 1982 to 9 March 1983, the midge population at Jasper Ridge was relatively stable—i.e., density of galls never exceeded 2 per 100 terminals and larval density did not exceed 20 per 100 terminals (Ehler et al., 1984). Life tables were constructed for six cohorts of *R. californica* galls collected on the following dates in 1982: 30 March (n = 144), 3 May (n = 47), 1 June (n = 85), 14 July (n = 124), 12 Aug. (n = 41) and 7 Oct. (n = 83). Because major trends in mortality/survival in each of the life tables were very similar, an average (n = 6) life table, based on 524 galls (5680 midge larvae), was calculated for a hypothetical cohort of 1000 individuals (Table 1). Three major sources of mortality were apparent: predation of eggs and neonate larvae, parasitization of endophagous larvae (i.e., inside the gall) and residual mortality of larvae. Midge survival from egg to adult was ca. 5% and the sex ratio was in favor of females.

The numbers of eggs and neonate larvae plus attendant mortality rates were estimated from figures given by Ehler et al. (1984). In this case, the value for lx was derived from the average gall size (assuming 100% survival from egg to endophagous larva) in an adjacent area (Woodside) which was heavily sprayed with malathion bait during the medfly eradication campaign. These sprays presumably destroyed most of the predators of these host stages and this apparently resulted in the consistently larger galls found in this zone (see next section). The value for dx was determined by subtraction. Because of the particular methods employed, the estimates obtained should not be viewed as giving a complete picture of events during this age interval. For example, predation was the only mortality factor estimated, even though other factors (e.g., infertility) are probably involved. In view of this, the value for lx should be regarded as an underestimate and that for dx as an overestimate. Nevertheless, the data do suggest that predation on eggs and neonate larvae (i.e., before gall formation) is of major importance in the population dynamics of the midge (see also Ehler et al., 1984). Although numerous predatory insects occur on the plant (Tilden, 1951a), it was not possible to determine which species were responsible for the mortality detected during this phase of the study.

Parasites destroyed ca. 38% of the endophagous larvae (25% real mortality). This overall parasitization rate is somewhat low and is not necessarily characteristic of the parasite guild in other parts of the host's range. Seven species of solitary parasites were reared from *R. californica* galls. *Torymus koebelei* (Huber) (Torymidae) is a primary ectoparasite; parasitization by this species ranged from 1 to 13%. A second torymid primary ectoparasite, *T. baccharidis* (Huber), was generally rare and never parasitized >2% of the host larvae. *Zatropis capitis* Burks (Pteromalidae) is a facultative secondary ectoparasite which parasitized from 0.9 to 6.5% of the hosts. The dominant species in the parasite guild was *Platygaster californica* (Ashmead) (Platygastridae), an egg-larval, primary endoparasite. This species parasitized from 1 to 36.2% of the larvae. *Mesopolobus* sp., another pteromalid facultative secondary ectoparasite, parasitized >10% of the hosts in March, but seldom parasitized >1% thereafter. The two remaining species were consistently rare: *Tetrastichus* sp. (Eulophidae), a primary endoparasite, never parasitized >1.1% of the hosts whereas *Eupelmus inyoensis* Girault (Eupelmidae), another facultative secondary ectoparasite, was collected on only one date (Oct. 7). Over 5% of the larvae (range: 0.5–9.5) were parasitized, but due to the condition of the material, it was not possible to attribute host mortality to any particular species listed above. Finally, total parasitization rate and rates for individual species were relatively constant over time; there was no convincing evidence for temporal density dependence.

The third major category of mortality was the residual—i.e., mortality of larvae which could not be directly attributed to parasites. The residual mortality rate was relatively high and probably has several components. Some hosts are presumably

Table 1. Average life table for *Rhopalomyia californica* at the Jasper Ridge Biological Preserve from March to October, 1982.*

x	lx	dxF	dx	100qx	100rx
Egg + neonate larva	1000	Predation	355	35.5	35.5
Endophagous larva	645	Parasitization			
		T. koebelei	41.9	6.5	4.2
		T. baccharidis	9	1.4	0.9
		Z. capitis	27.7	4.3	2.8
		P. californica	106.4	16.5	10.6
		Mesopolobus sp.	20	3.1	2.0
		Tetrastichus sp.	2.6	0.4	0.3
		E. inyoensis	3.2	0.5	0.3
		Undetermined	34.8	5.4	3.5
		Total	245.7	38.1	24.6
		Residual	341	52.9	34.1
Pupa	58.3	Residual	6.2	10.6	0.6
Adult	52.1	(0.61♀♀:0.39♂♂)	947.9	—	94.8

*Key to symbols: x = developmental stage, lx = number entering stage x, dxF = mortality factor, dx = number dying during stage x, 100qx = dx ÷ lx for that stage (apparent mortality) and 100rx = dx/lx for the initial cohort (real mortality). See Ehler (1982) and Ehler et al. (1984) for details of materials and methods.

killed by adult parasites—e.g., by host feeding, probing with the ovipositor (see also Force, 1974)—and this would not be detected by the methods employed in this study. Supernumerary parasitization is common at times and this could possibly result in death of all occupants (host and parasites) in a given chamber. For these reasons, the data for parasitization in Table 1 are probably a conservative reflection of the actual impact of parasites. I also suspect that many gall inhabitants (both hosts and parasites) were inadvertently killed during collecting and processing of galls. Recent dissections of fresh galls (prior to midge emergence) collected in Yolo and Solano Counties revealed that up to 10% of the chambers were empty. In other words, some mortality had occurred prior to sampling, reinforcing the belief that residual mortality has numerous components, as opposed to being strictly an artifact of sampling technique.

Impact of Malathion-Bait Sprays

A massive outbreak of *R. californica* occurred at Woodside following 24 applications of malathion bait. At the height of the outbreak (Oct. 1982), midge population levels were ca. 90X greater than those observed at Jasper Ridge. This classic secondary outbreak evidently resulted from the wholesale destruction of natural enemies of the midge (Ehler et al., 1984). I report here on a more subtle or indirect effect of the sprays. The destruction of natural enemies (probably predators) evidently allowed greater survival of eggs and neonate larvae which in turn allowed more larvae to enter available buds and this presumably resulted in comparatively larger galls in the spray zone. Although this effect was evident on all sample dates in 1982, the data for October were particularly striking (Figure 1). At Jasper Ridge, the

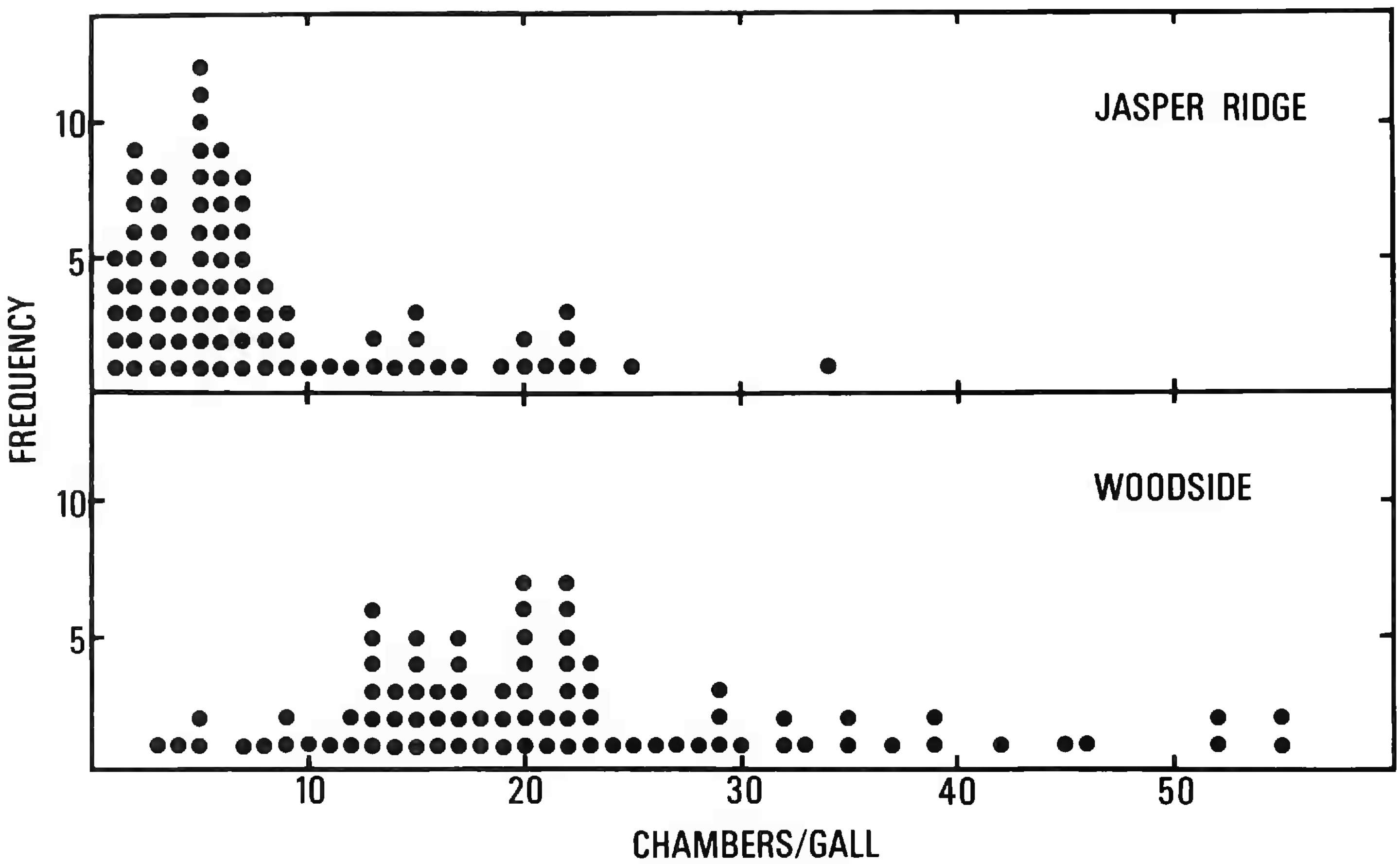

Figure 1. Frequency distribution of galls according to size (chambers per gall) at Jasper Ridge (control) and Woodside (medfly spray zone). Galls were collected on 7 October 1982; each dot represents one gall (n = 83 for both sites).

median number of chambers per gall was 5 compared to 19 at Woodside; the average number of chambers per gall at Woodside (21.9) was >2X that at Jasper Ridge (8.1). In other words, the malathion-bait sprays altered the spatial structure of the midge population. Conversely, the data suggest that natural enemies can play a major role in determining the spatial structure of a host population in nature. In view of these findings, the value of gall size as an index of host-plant quality, while perhaps intuitively appealing, must be questioned. This may also apply to midge populations in Texas and Australia because native generalist predators on related *Baccharis* spp. could produce a similar effect. Finally, the influence of an altered spatial structure of a host population on the behavior and performance of a natural enemy should be investigated.

Rhopalomyia As a Biological-Control Agent

The results from Woodside suggest that *R. californica,* when introduced without its natural enemies, has considerable potential as a biological-control agent against weedy *Baccharis* spp. in Texas and Australia. The host plants at Woodside were so devastated (by the midge and other phytophagous species) that sampling had to be discontinued after October 1982. This can be taken as an indication of the kind of impact the midge might have in biological control of weeds. In future projects, deliberate disruption of herbivore populations in the native home of a target weed might serve as an aid in selecting candidate natural enemies for further study.

The selection of effective natural enemies for biological control of weeds has received considerable attention in recent years (Harris, 1973; Goeden, 1983). In this context, the case of *R. californica* is relevant to a current controversy over the use of coevolved versus "new"' exploiter-victim associations. Hokkanen and Pimentel (1984) argued that new associations should be the preferred method of selecting natural enemies; this recommendation was based on the hypothesized lack of coevolved, interspecific balance which attends such associations. However, Goeden and Kok (1986) challenged these findings and suggested that new exploiter-victim associations offer limited opportunities for biological control, especially for non-cactaceous weeds. Although controversial, I believe that the Hokkanen-Pimentel thesis should be carefully considered and empirically tested whenever possible. The introduction of *R. californica,* derived from *B. pilularis* in California, into Australia and Texas for control of related *Baccharis* spp. should provide some key information on this question.

Acknowledgments

I thank A. Grundmann and associates at Stanford University for the opportunity to conduct research at the Jasper Ridge Biological Preserve and B. Alvarado-Rodriquez, P. C. Endicott, M. B. Hertlein, H. P. Sauter and K. Thorarinsson for assistance in collecting and analyzing the data. K. Thorarinsson, W. A. Palmer and P. Boldt reviewed an earlier version of the manuscript. Portions of this research were supported by the California Department of Food and Agriculture (Standard Agreement 1779).

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